The Beagle, Records of the Museums and Art Galleries of the Northern Territory, 2011 **27**: 189–204

The natural history of mudskippers in northern Australia, with field identification characters

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ABSTRACT

We provide field identification characters and report on the natural history of mudskippers (Gobiidae: Oxudercinae) in Cairns, Darwin, Derby and Broome, northern Australia. Nine species in four genera are recorded (*Boleophthalmus birdsongi, B. caeruleomaculatus, Periophthalmodon freycineti, Periophthalmus argentilineatus, P. darwini, P. minutus, P. novaeguineaensis, P. takita* and *Scartelaos histophorus*). The intertidal zonation of mudskippers conforms to previously reported patterns, but subtle differences in habitat preference are observed at both intraspecific and intrageneric levels, underlining the need for in-depth investigation of habitat selection by mudskippers. Although most species inhabit littoral mudflats, some show possible habitat expansion: juvenile *Periophthalmodon freycineti* are found occasionally in pools on a sandy shore, and a population of *Periophthalmus minutus* is found to be established in a marginal mangrove habitat (a salt flat behind a pioneer mangrove assemblage). Burrow confinement during high tide is confirmed for both species of *Boleophthalmus*, two *Periophthalmus* (*P. minutus* and *P. novaeguineaensis*) and *Scartelaos*, but not for *Periophthalmodon* or the other *Periophthalmus* species. Territory formation is described for *S. histophorus*.

Keywords: mudskipper, Oxudercinae, northern Australia, field identification, distribution, habitat condition, natural history

INTRODUCTION

The term mudskipper usually refers to those amphibious gobies that move about actively on the exposed mudflats of creeks, estuaries and coastal areas during low tide (Clayton 1993; Graham 1997; Graham *et al.* 2007). These fishes belong to the gobiid subfamily Oxudercinae, which includes 40 species in 10 genera (Murdy 1989; Lee *et al.* 1995; Murdy & Takita 1999; Darumas & Tantichodok 2002; Larson & Takita 2004; Jaafar & Larson 2008; Jaafar *et al.* 2009) and are distributed from eastern Asia, the South Pacific islands and northern Australia, westward across South-east Asia and the Arabian Peninsula to both the east and west coasts of Africa (Murdy 1989).

Mudskippers are often one of the dominant ecological components on tidal flats, and they play an important ecological role as carnivores and as preferred prey for many avian predators (Clayton 1993). As such, these fishes contribute to the maintenance of the integrity and health of mudflat ecosystems, which are often very vulnerable to negative human impacts, but offer significant ecological services (Reise 1985; Costanza *et al.* 1997). For these reasons and because of their biological peculiarity as amphibious fish, mudskippers have been investigated from various aspects; for example, their life on mud, locomotory mechanics, air-breathing capabilities, burrowing and reproductive behaviour (e.g. Atkinson & Taylor 1991; Harris 1960; Ishimatsu *et al.* 1998, 2007, 2009; MacNae 1968; Takeda *et al.* 1999; Tamura *et al.* 1976; Zhang *et al.* 2003). Recently their ability to produce vocalisations has been confirmed (Polgar *et al.* 2011). In addition, mudskippers are an invaluable source of information for insights into vertebrate invasion from an aquatic to terrestrial environment (Ishimatsu & Gonzales 2011).

Twelve species of oxudercine gobies belonging to six genera are known from tropical and subtropical northern Australia, where numerous mudflats and other soft substrates are located in sheltered bays, estuaries and areas protected by coral reefs or mangrove forests (Murdy 1989; Larson & Williams 1997; Larson & Takita 2004; Hoese & Larson 2006; Jaafar & Larson 2008). Notwithstanding the abundance of mudskippers in these habitats, biological data are scarce and generally restricted to species inhabiting the east coast of Australia. Milward (1974) studied the morphology, physiology, distribution, food and feeding habits, and habitat conditions of five mudskipper species in areas from Cairns to Brisbane, Queensland. Nursall (1981) provided notes on the behaviour and habitat of one *Periophthalmodon* and four *Periophthalmus* species near

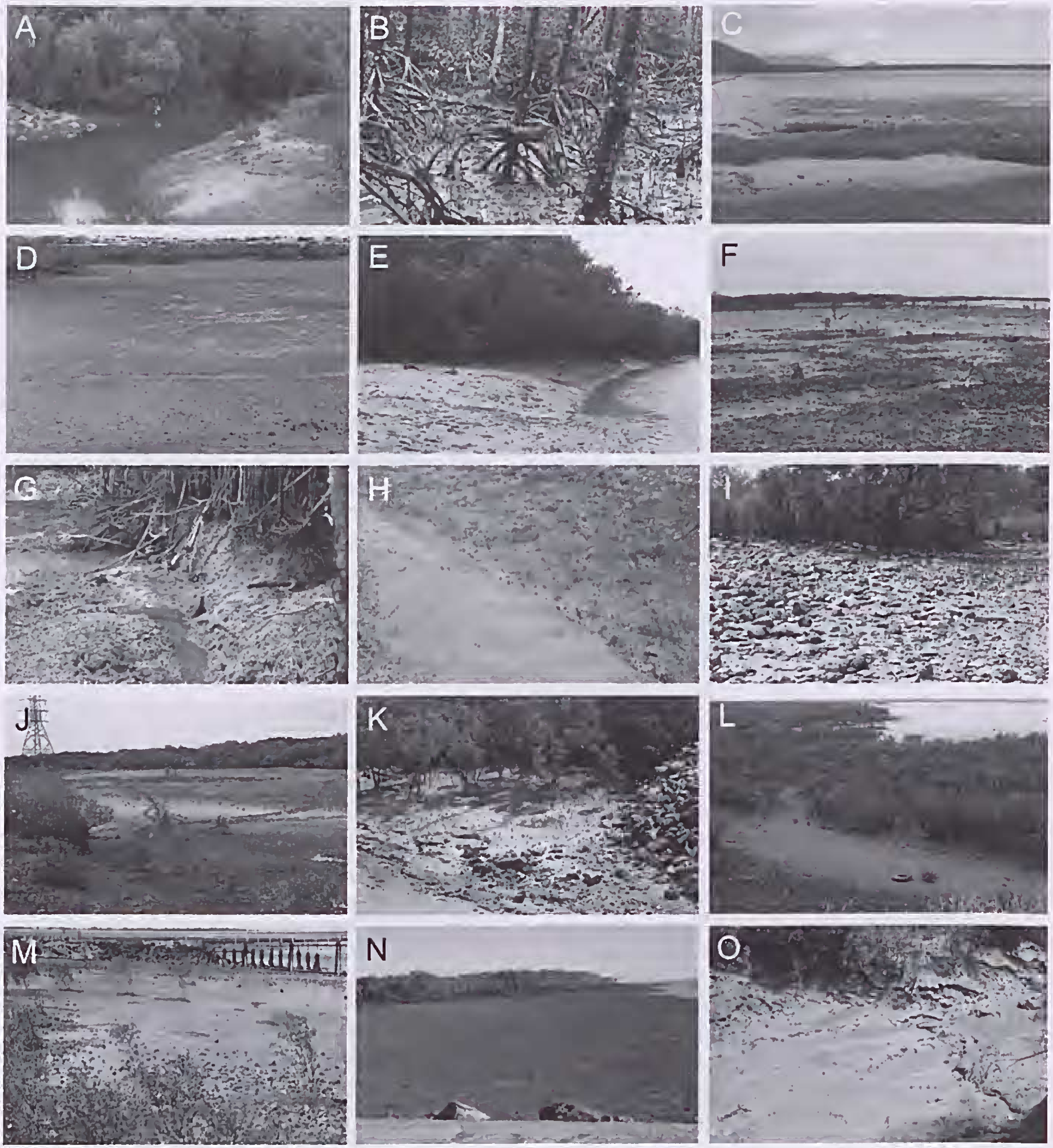

Fig. 1. Habitats of mudskippers in northern Australia. The labels correspond to the site designation given in Table 1 (**A-C**, Cairns; **D-K**, Darwin; **L**, Broome; **M-O**, Derby). See Table 1 for site descriptions.

Townsville, Queensland. Townsend & Tibbetts (1995) studied the distribution and the seasonal occurrence of *Scartelaos histophorus* (Valenciennes) in Brisbane, and Townsend & Tibbetts (2005) reported the behaviour and sexual dimorphism of *S. histophorus*.

Thus, the aim of this study was to collect natural history information on the distribution, habitat conditions and lifestyle of mudskippers in four locations of northern Australia, from the east coast of Queensland through the Northern Territory to northern Western Australia. Key characters useful for field identification of mudskippers are also provided to aid further investigations of mudskippers in these regions.

MATERIALS AND METHODS

Study Sites. Field surveys were conducted on tidal flats along the coasts of Cairns in Queensland, Darwin in the Northern Territory, and Derby and Broome in Western Australia, from 2000 through 2004 (Table 1). The mudflats in Darwin were the most extensively and frequently investigated. All localities are tropical with monthly mean temperature being around 30°C (26–38°C depending on locality) throughout the year, and highest rainfall during the months of November/December through February/March (a monsoonal climate; http://www.bom.gov.au/climate/data/index.shtml).

In Queensland mudskippers were surveyed at Yorkeys Knob (Site A, Fig. 1A), near Cairns Airport (Site B, Fig. 1B) and at Esplanade Beach, Cairns (Site C, Fig. 1C). In the Northern Territory the study sites around Darwin included a beach in Darwin Harbour (Site D, Fig. 1D), Ludmilla Creek (Site E, Fig. 1E), mudflats in the Howard River estuary (Site F, G, H, Fig. 1F, G, H), a sloping muddy boulder-strewn shore at Channel Island (Site I, Fig. 1I) and two mudflats (Site J, K, Fig. 1J, K) on the right bank of Middle Arm, Port Darwin. In Western Australia the study sites were a beach facing Roebuck Bay in Broome (Site L, Fig. 1L) and three locations in and outside of Derby Harbour (Site M, N, O, Fig. 1M, N, O) in the Fitzroy River estuary. Macrotidal conditions existed at all sites, reaching more than 8 and 10 m in Port Darwin and Derby, respectively.

Field Observations. Living mudskippers were photographed in their habitats to record body shape and colour patterns. Body colour and shape of freshly caught fish were also recorded immediately after fixation in 10% formalin solution to assist with field identification criteria. Their behaviour was observed and recorded with binoculars

Table 1. Study sites and times for mudskipper surveys in northern Australia.

	Site description	**Month**					
		Jan.	**Feb.**	**Mar.**	**Jul.**	**Aug.**	**Nov.**
Cairns, Queensland							
Yorkeys Knob	*Site A:* Narrow mud banks of the Moon River estuary (Fig. 1A 16°48’07”S, 145°42’49”E).	X			X		
Cairns Airport	*Site B:* Mangrove forest reserve by airport (Fig. 1B), crossed by Middle Creek (not shown in photograph 16°52’46”S, 145°45’34”E).	X			X		
Esplanade Beach	*Site C:* Open muddy beach and mudflats, Cairns (Fig. 1C), partially covered by sand (not shown in photograph 16°54’50”S, 145°46’21”E).	X		X	X		X
Darwin, Northern Territory							
Darwin Harbour	*Site D:* Mud and sandy boulder-strewn tidal flats, bordered landward by mangrove forest (Fig. 1D 12°26’50”S, 130°51’07”E).		X			X	X
Ludmilla Creek	*Site E:* Narrow mud banks along Ludmilla Creek mouth, bordered by mangrove forest (Fig. 1E 12°24’44”S, 130°50’14”E).	X	X		X	X	X
Howard River estuary	*Site F:* Open, level mudflats on the left bank of Howard River mouth (Fig. 1F 12°21’39”S, 131°01’21”E).	X		X	X		X
	Site G: Landward mangrove border of Site F, with 1–2 m tall mud mounds present , adjacent to eucalypt forest (Fig. 1G 12°21’39”S, 131°01’21”E).	X			X		
	Site H: Muddy ditches running from adjacent fish ponds, sparsely covered by the halophyte, *Suaeda arbusculoides* (Fig. 1H 12°21’39”S, 131°01’21”E).			X	X		
Channel Island	*Site I:* Open boulder-strewn muddy shore on west coast of Channel Island (Fig. 1I 12°33’24”S, 130°51’43”E).	X	X	X	X	X	X
Middle Arm	*Site J:* Open mudflat (Fig. 1J) separated by approx. 150 m width mangrove belt from right bank of Middle Arm; mudflat sparsely vegetated by *S. arbusculoides* and surrounded by mangroves, mainly *Avicennia marina* and *Ceriops australis* (12°33’41”S, 130°52’56”E).	X	X	X	X	X	X
	Site K: Narrow mudflat on right bank opposite Channel Island, densely covered by aerial roots of *A. marina* and strewn with boulders (Fig. 1K 12°33’12”S, 130°52’35”E).	X	X				
Broome, Western Australia							
Roebuck Bay	*Site L:* Open muddy beach, with muddy lower zone and sandy upper zone (Fig. 1L 17°58’16”S, 122°14’09”E)		X		X		
Derby, Western Australia							
Fitzroy River estuary	*Site M:* Boulder-strewn mudflat within Derby Harbour (Fig. 1M 17°17’33”S, 123°36’29”E).		X	X	X		
	Site N: Open mudflat bordered landward by mangrove forest, outside Derby Harbour (17°17’33”S, 123°36’29”E).		X	X	X		
	Site O: Small mudflat bordered by mounds in mangroves at Site N (17°17’33”S, 123°36’29”E).		X	X	X		

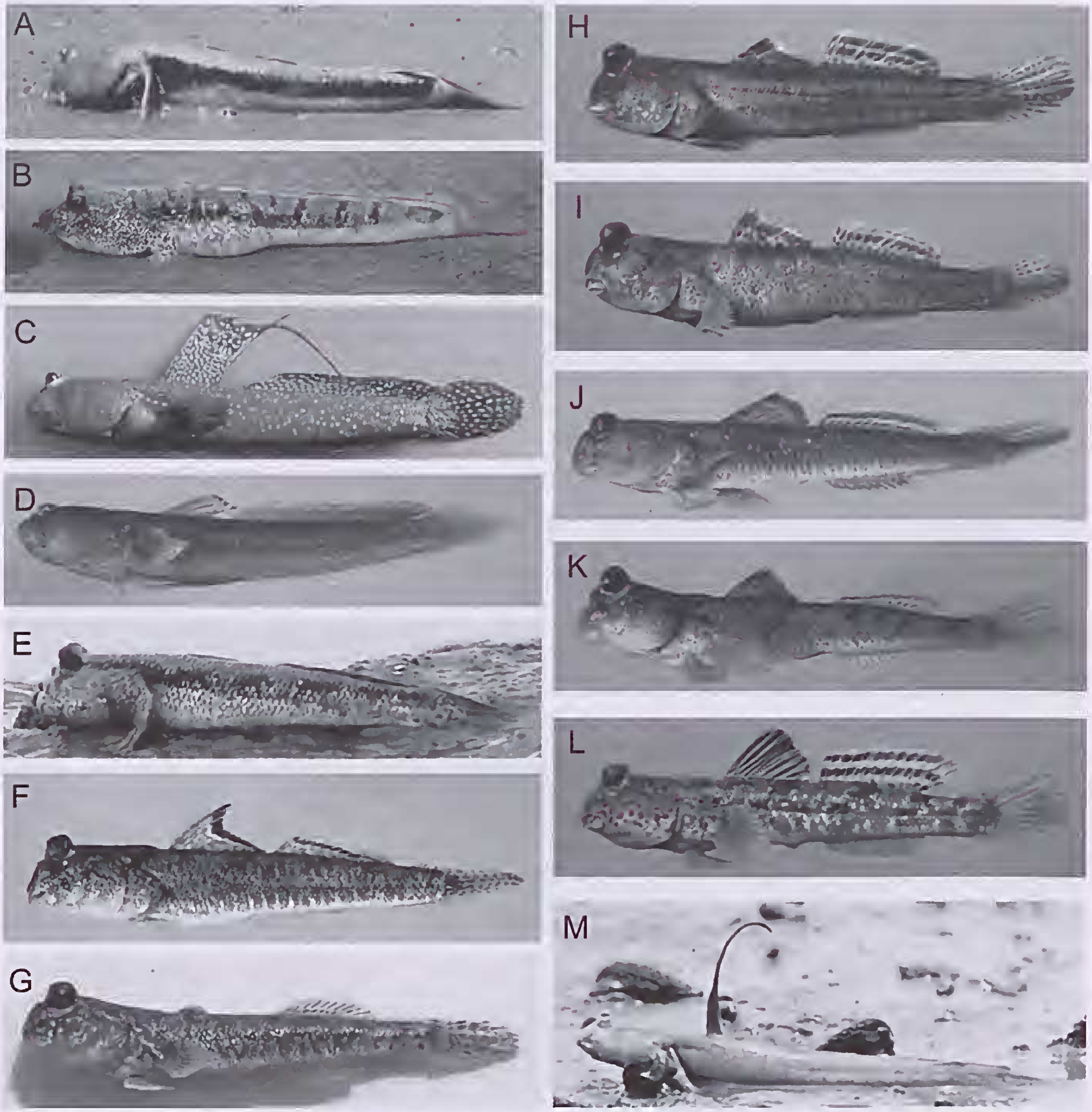

Fig. 2. Living and freshly dead mudskipper species collected in northern Australia. Size is given as total length. **A**, *Boleophthalmus birdsongi*; **B**, *B. birdsongi* juvenile (ca. 50 mm); **C**, *Boleophthalmus caeruleomaculatus* (185 mm); **D**, *B. caeruleomaculatus* juvenile (73 mm); **E**, *Periophthalmodon freycineti*; **F**, *Periophthalmus argentilineatus* (85 mm); **G**, *Periophthalmus darwini* (52 mm); **H**, *Periophthalmus minutus* (male: 55 mm); **I**, *Periophthalmus minutus* (female: 53 mm); **J**, *Periophthalmus novaeguineaensis* (male: 57 mm); **K**, *Periophthalmus novaeguineaensis* (female: 64 mm); **L**, *Periophthalmus takita* (71 mm); **M**, *Scartelaos histophorus*.

and a video camera. Field surveys were usually conducted around times of low spring tides when the habitats were exposed, while some surveys were undertaken at high tide to confirm whether mudskippers remained emerged or confined in their burrows. Mudskipper emergence or burrow confinement at high tide was judged from a comparison of fish numbers in the same habitat at high and low tide, and when possible from observation of mudskippers emerging from burrows at ebb tide. Burrow water salinity was measured with a hand-held salinometer (S/Mill-E; ATAGO, Japan).

Fish Collection. For collecting *Boleophthalmus*, cylindrical pitfall traps (PVC pipe with one end closed at an angle) were used; hook and line with bait for *Periophthalmodon*; while *Periophthalmus* and *Scartelaos* were collected by dip net or by hand. Collected mudskippers were identified following Murdy (1989), Larson & Takita (2004) and Jaafar & Larson (2008). Voucher specimens are deposited at the Museum and Art Gallery of the Northern Territory, Australia and the National Museum of Nature and Science, Tokyo, Japan.

RESULTS

Species Collected. A total of nine mudskipper species was collected in this study (Fig. 2). This included two species of *Boleophthalmus* (*B. birdsongi* Murdy, Fig. 2A,B and *B. caeruleomaculatus* McCulloch & Waite, Fig. 2C,D), one species of *Periophthalmodon* (*P. freycineti* (Valenciennes), Fig. 2E), five species of *Periophthalmus* (*P. argentilineatus* Valenciennes, Fig. 2F, *P. darwini* Larson & Takita, Fig. 2G, *P. minutus* Eggert, Fig. 2H,I, *P. novaeguineaensis* Eggert, Fig. 2J,K and *P. takita* Jaafar & Larson, Fig. 2L) and one species of *Scartelaos* (*S. histophorus* (Valenciennes), Fig. 2M). Their distribution in the sites surveyed is provided in Table 2.

Field Identification. The key characters most useful for field identification of species collected in this study are summarised in Table 3. It should be noted that in this paper 'juvenile' refers to small, clearly immature individuals with an indistinct colour pattern.

Adult *B. birdsongi* (Fig. 2A) and *B. caeruleomaculatus* (Fig. 2C) are distinguishable by body size, dorsal fin morphology and fin and body colour pattern as given in Table 3. The largest *B. caeruleomaculatus* we collected measured 144 mm in standard length (SL) and 185 mm in total length (TL), in comparison to 115 mm SL and 138 mm TL of the largest *B. birdsongi* specimen. Smaller individuals of the two species showed different colour pattern and morphology from adults. Juvenile *B. birdsongi* (Fig. 2B) was wholly greyish in body colour with dark-brown irregularly-shaped vertical bars, but had no horizontal dark stripe laterally on the body. One juvenile *B. caeruleomaculatus* (73 mm TL, Fig. 2D) was grey in body colour and had no particular pattern on the body (note that the photograph of Fig. 2D was taken several days after specimen preservation so that it does not represent the colour pattern of the live fish).

Periophthalmodon freycineti specimens (Fig. 2E) are discernible from *Periophthalmus* species by their larger maximum size, evenly grey-brown body colour and the dorsal fins without a distinct pattern. The black stripe coursing posteriorly from the eye to the caudal peduncle described by Murdy (1989) is conspicuous in juveniles but not always visible in adults.

Periophthalmus argentilineatus (Fig. 2F) has a distinct colour pattern and a first dorsal fin (DF1) morphology as given in Table 3. Vertical white lines on the side of the body, which are also present in *P. minutus* (Fig. 7A,D), are distinctive in *P. argentilineatus*. *Periophthalmus darwini* (Fig. 2G) is distinguished from other species of *Periophthalmus* by the very small DF1 and the space between the DF1 and the second dorsal fin (DF2) being greater than the DF1 basal length. *Periophthalmus minutus* (male Fig. 2H, female Fig. 2I) shows sexual dichromatism: the dorsal fins are brighter red in colour (and a little larger

Table 2. Habitat characteristics of nine species of mudskippers in northern Australia. BR, Broome; CA, Cairns; DA, Darwin; DE, Derby; a, adults; j, juvenile. Letters in parentheses correspond with labels in site photographs, Figure 1. *Definition: 'level' here is horizontal, parallel to the horizon; 'sloping' has an angle with the horizon; 'smooth' means homogeneous substrate, with no major convex or concave landmarks; 'irregular/rough' is the opposite, with erosion, stones, pneumatophores and other objects to make the surface not 'smooth'.

Species		**Habitat characteristics**		
	Occurrence confirmed	**Topography***	**Height in intertidal**	**Substrate**
Boleophthalmus birdsongi (a)	DA(D,E,F), DE(N)	level or sloping, with smooth or irregular surface	low	mud or muddy sand
B. birdsongi (j)	DA(H,J)	level; smooth	highest	mud
Boleophthalmus caeruleomaculatus	DA(F), DE(N)	level; smooth	low	mud
Periophthalmodon freycineti (a)	CA(B,C), DA(E)	level or sloping	low	mud
Periophthalmodon freycineti (j)	CA(B,C)	mangrove forest floor or shallow water pool	middle	mud or sand
Periophthalmus argentilineatus	CA(A,B), DA(D,E), BR(L)	level or sloping, mangrove forest floor	high and low	mud
Periophthalmus darwini	DA(E,G,I,K), DE(O)	sloping or with mounds with surface inequalities available for refuges (e.g., rocks, pneumatophores)	highest	mud
Periophthalmus minutus	DA(F,H,J)	level and smooth	highest	mud
Periophthalmus novaeguineaensis	DA, DE(M,O)	sloping or with mounds with surface inequalities available for refuges (e.g., rocks, pneumatophores)	highest	mud
Periophthalmus takita	DA(E,F)	level or sloping	low	mud
Scartelaos histophorus	CA(C), DA(F), DE(N), BR(L)	level	low	mud

Table 3. Field identification characters for nine mudskipper species from northern Australia. Note that juvenile *Boleophthalmus* differ in colour pattern from adults (see text).

Species	Body morphology and colour pattern	Dorsal fin (DF) morphology and colour pattern		Figure
		First DF	Second DF	
Boleophthalmus birdsongi	Maximum size smaller than *B. caeruleomaculatus*. Horizontal black band on mid-side of body usually visible.	Black, paler proximally. Spines usually shorter than in *B. caeruleomaculatus* (i.e. less than body depth).	Yellow fin margin, blackish stripe along centre of fin.	2A
Boleophthalmus caeruleomaculatus	Body greyish brown with bright blue speckles. Blue skin at base of eyeball.	Greyish background colour, covered with small blue spots and speckles. 4th spine may be elongated and filamentous; entire fin height greater than body depth in large adults.	Same colour as DF1 but spots tending to be more regularly spaced.	2C
Periophthalmodon freycineti	Large body size (can be over 200 mm SL). Dark grey to brownish grey body colour, paler ventrally, small pale blue to whitish spots scattered over side of head; broad black horizontal stripe running from behind eyes to upper part of caudal fin base (stripe not always displayed).	Short fin base; wide interdorsal space. Grey in colour, with whitish to dull yellow margin.	Evenly dark grey (can be pinkish grey to brownish) in colour.	2E
Periophthalmus argentilineatus	White speckling on side of head. Side of body with numerous narrow silvery white vertical stripes, most conspicuous on ventral half of body (fading quickly under stress or after fixation.	Tall and pointed anteriorly. Sub-marginal white-edged black stripe; rest of fin dull red to reddish brown with many white spots.	Reddish distal margin; submarginal white-bordered dark band and basal half of fin of similar colour pattern to DF1.	2F
Periophthalmus darwini	Small and slender; maximum size 45 mm SL.	Reduced in size, with interdorsal space very wide. Dull brown with pale margin.	Fin membranes with few rows of brownish streaks and small spots.	2G
Periophthalmus minutus	Snout steeper than other *Periophthalmus*. Light brown body with widely scattered small dark brown speckles; many vertical white lines on side of body (fading quickly after fixation).	Fin triangular. In male, fin reddish with broad white margin, with small dark red to red-brown spots and streaks on membranes. Female with submarginal brown to reddish band, rest of fin duller than in male.	Broad white margin in both sexes, with brownish (female) to reddish (male) submarginal stripe and medial brown to greyish brown stripe; small dark brown spots along fin ray bases.	2H (male) 2I (female)
Periophthalmus novaeguineaensis	Grey to brown body, lighter ventrally. Head and body covered with numerous dark brown and blue spots and speckles.	White fin margin (brighter in male) with inframarginal red-brown to dark brown stripe; rest of fin bright red.	Translucent pinkish to pale brownish, with brown inframarginal stripe and series of dark brown streaks and speckles basally; margin usually transparent.	2J (male) 2K (female)
Periophthalmus takita	Body grey to greyish brown, with conspicuous orange, red brown and dark brown spots (and smaller white spots) on side of body.	Fin large, with somewhat rounded margin. Reddish brown to dark brown with pale spines.	Submarginal and medial blackish horizontal stripes on white background; basal part of fin with dark spots.	2L
Scartelaos histophorus	Slender body, light blue-grey in colour with fine blackish speckles and narrow vertical lines on side.	Dark brown, elongate and 'mast-like'; interdorsal space much wider than DF1 base.	Pale grey to transparent.	2M

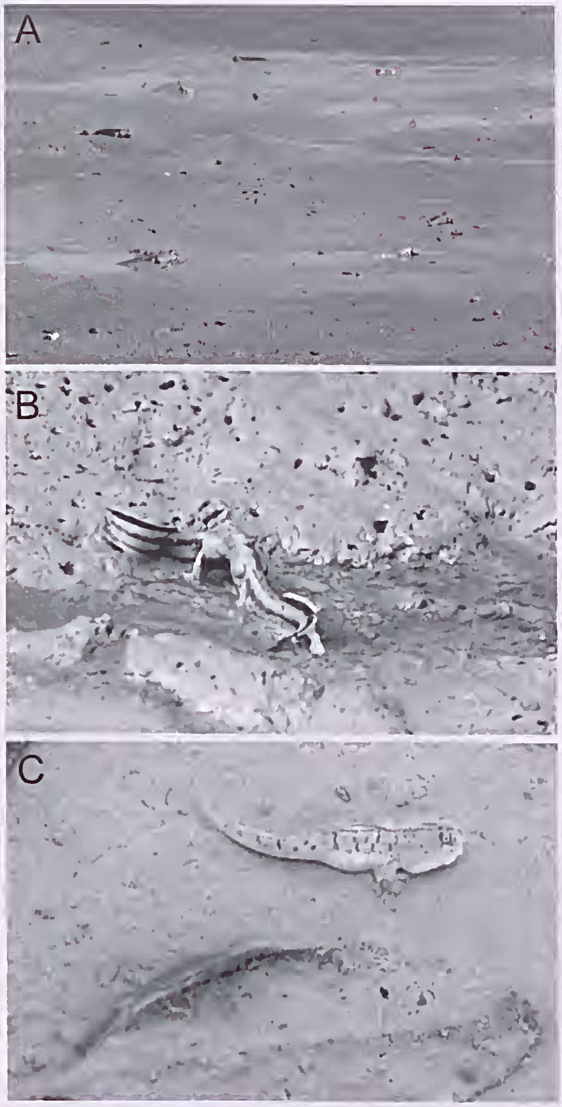

Fig. 3. *Boleophthalmus* species in their habitats. **A**, *B. caeruleomaculatus* on Derby coastal mudflat (Site N, July 2002); **B**, two *B. birdsongi* fighting on a sloping mudflat in Darwin Harbour (Site D, Nov. 2000); **C**, *B. birdsongi* juvenile in a pool in Middle Arm, Port Darwin (Site J, March 2003).

in size) in males than in females. The margins of these fins are white in both sexes, but become semi-transparent immediately after fixation.

Periophthalmus novaeguineaensis also shows sexual dichromatism (male Fig. 2J, female Fig. 2K): it has reddish dorsal fins, with the white colour of the DF1 and DF2 margins brighter in males (Fig. 2J). The species is easily recognisable in the field. The body colour becomes darker in males when mating (Fig. 8C). The anal fin is dark in larger males (Fig. 2J) and paler in females (Fig. 2K). *Periophthalmus takita* (Fig. 2L) differs from its congeners in having a large DF1 and two distinct horizontal dark stripes on the DF2. The anal fin and the ventral edge of the caudal fin are yellow in colour. All species of *Periophthalmus* usually show some oblique dark bars on the side of the body, though these markings are occasionally faint or indiscernible.

Scartelaos histophorus (Fig. 2M) is easily identified in the field on the basis of the body morphology and colouration (Table 3). The fish frequently erect the mast-like DF1. Males are larger than females.

Habitat conditions and lifestyle.

***Boleophthalmus birdsongi* and *B. caeruleomaculatus*.** The distribution of *B. birdsongi* was observed to be wider than that of *B. caeruleomaculatus* (Table 2). *Boleophthalmus birdsongi* occurred on every mudflat in the low intertidal zone in Darwin and Derby, inhabiting either sloping and rough (Fig. 3B) or level and smooth mudflats and muddy sandflats (see Table 2 for definition of topographical terms). *Boleophthalmus caeruleomaculatus* was restricted to mudflats that were always wet, smooth, comparatively level and more extensive than other mudflats studied (Fig. 3A, Table 2). Adults of both species of *Boleophthalmus* maintained a burrow for retreat when frightened or when the tide covered the habitat (Table 4). Deduced from the distinctive side to side movement of the head on exposed mudflats, both *B. birdsongi* and *B. caeruleomaculatus* likely foraged for surficial algae and diatoms, as known for all other congeners studied (Clayton 1993), during low tide within a territory around the burrow. Both species performed an aggressive display (Fig. 3B) when protecting the territory or chasing away approaching conspecifics. Courtship displays were observed in July (*B. caeruleomaculatus*) and August and November (*B. birdsongi*) (Table 4).

Habitat separation with growth was confirmed for *B. birdsongi* but not for *B. caeruleomaculatus*. Juveniles of *B. birdsongi* measuring from 22 to 66 mm TL (Figs 2B and 3C) were found in the intertidal zone close to the high water line of spring tide (HWS) during spring tide in March, July and November at Sites H and J; two sites where adult *B. birdsongi* were never observed. The juveniles of *B. birdsongi* disappeared from these high locations during neap tide when the habitat remained exposed by the tide and became dry. Unlike *B. birdsongi,* juvenile *B. caeruleomaculatus* of about 70 mm TL and smaller (Fig. 2D) occurred together with adults in March and July in the Howard River estuary (Fig. 1F; Site F) and on the Derby coast (Fig. 1N; Site N).

***Periophthalmodon freycineti*.** Adults of *P. freycineti* (Fig. 4A) inhabited open mudflats as in site C but also occurred on stream banks in Sites B and E. Juveniles were found in March in small shallow pools in the sandy part of Site C (Fig. 4B) or on the forest floor of the Red Mangrove, *Rhizophora stylosa*, at Site B (Table 2); both areas of which were landward of the adult's habitat. This suggests that *P. freycineti* showed a clear habitat separation between different size classes (Table 2). Adults of *P. freycineti* were often found beside or near their burrows irrespective of

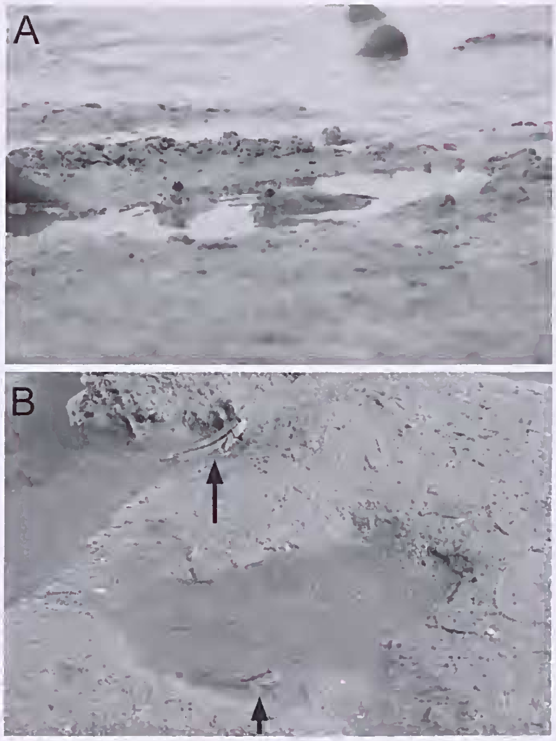

Fig. 4. *Periophthalmodon freycineti* on the Esplanade mudflat, Cairns (Site C). **A**, pair of *P. freycineti* in burrow (Nov. 2000); **B**, *P. freycineti* juveniles (indicated by arrows) in shallow pools (March 2003).

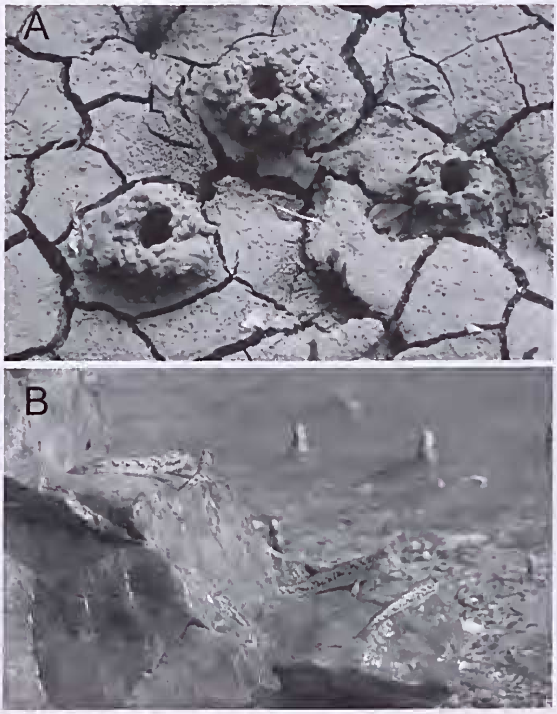

Fig. 5. *Periophthalmus argentilineatus*. **A**, burrow openings with turrets in mangrove forest in Cairns (Site B, July 2001); **B**, *P. argentilineatus* waiting for tide to ebb, Darwin Harbour (Site D, February 2004).

seasons (Fig. 4A). During habitat inundation by the tide, numerous if not all *P. freycineti* were seen along the water's edge. In November 2000 we observed at Site C, that pairs of *P. freycineti* alternately gulped air and dove into their burrows (Table 4) as observed for *P. schlosseri* (Ishimatsu *et al.* 1998, 2009), suggesting air storage in egg chambers (Ishimatsu *et al.* 2009) and biparental embryonic care in both species. HKL confirmed the occurrence of this behaviour in Cairns during December 2006 and March 2010.

Periophthalmus argentilineatus. *Periophthalmus argentilineatus* migrates across tidal flats with changing tides. At high tide, this species rested on exposed sediment, rocks (Fig. 5B) or roots of the Red Mangrove *Rhizophora stylosa*, as observed at Sites D, E, and L (Table 2). As the tide ebbed, the fish followed the receding water down to the mudflats. A similar seaward migration during ebb tide was seen along the creek bank at Site A. The fish returned to the higher zones or the mangrove forest with the rising tide, probably after foraging on open tidal flats. Burrows with two or three turreted openings (Fig. 5A) were abundant at Site B throughout the year, even though only a few *P. argentilineatus* were observed near their burrows at low tide. We were unable to confirm use and function of their burrows, located abundantly on the mangrove forest floor (Table 4).

Periophthalmus darwini. *Periophthalmus darwini* was usually found in the highest intertidal zone (Table 2), although some individuals were occasionally observed on lower areas. It inhabited steep mounds present on mud at Sites G and O, a rock-strewn muddy shore at Site I, or a sloping mudflat covered by the pneumatophores of the mangrove *Avicennia marina*, at Site K. Fish were seen to forage high on the mud mound surfaces, at the seaward front of the forest floor above mounds or among dense aerial roots of the mangrove (Fig. 6A). At Site I, *P. darwini* foraged on mud or sand accumulating between rocks. Individuals of *P. darwini* resting on a mud mound would swiftly climb up it (Fig. 6B) and take refuge in the mangrove vegetation when frightened. Burrow excavation behaviour was confirmed only once in July, 2001, at Site I (Fig. 6C). The burrow opening was about 1 m below HSW. A comparison of the number of presumed *P. darwini* burrows and the number of fish foraging during low tide suggests that the majority of, if not all, *P. darwini* did not possess a burrow and remained on land during high tide (Table 4). In fact, *P. darwini* was seen to remain on land or on exposed aerial Red Mangrove roots among rocks during high tide (Fig. 6D). Courtship has not been observed, although abundant juvenile *P. darwini* of about 10 mm TL were found in February 2003 and 2004 at Site I (Table 4).

Periophthalmus minutus. As with *P. darwini*, *P. minutus* (Fig. 7A) inhabited the highest intertidal zone at Sites F, H and J. Site J was inundated by the tide for only a few days in each tidal cycle and remained un-inundated for more than 10 days during neap tide, resulting in extreme dehydration of the surface mud. Site F was similar to Site J only in its

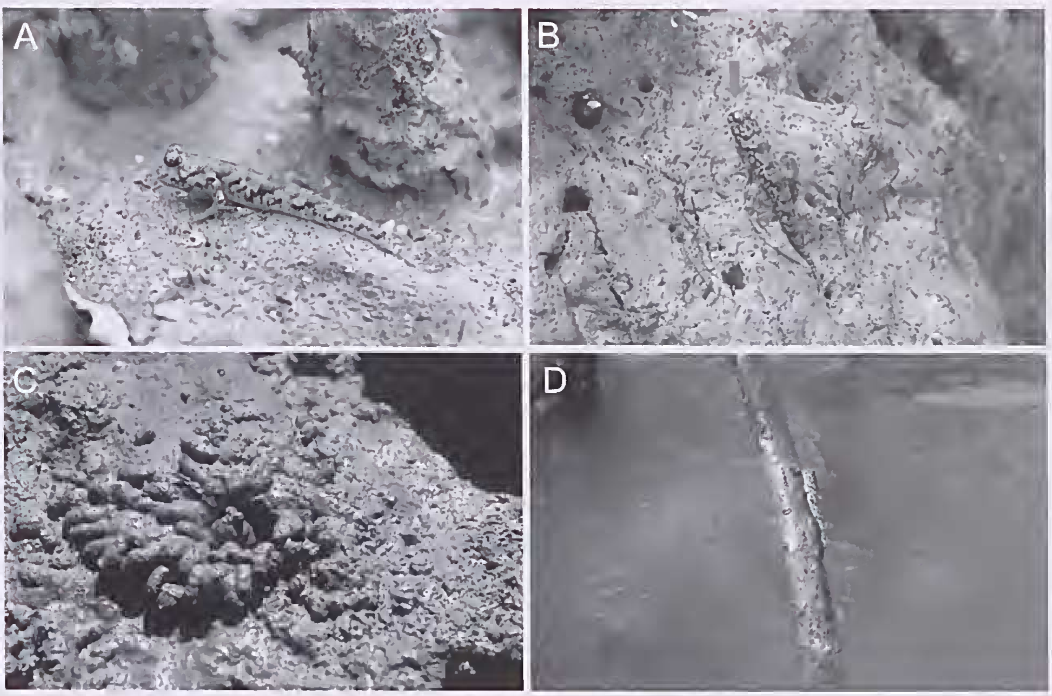

Fig. 6. *Periophthalmus darwini.* **A**, *P. darwini* crawling between dense aerial roots of *Avicennia marina*, Middle Arm, Port Darwin (Site K, Jan. 2002); **B**, *P. darwini* (arrow) climbing up a steep mud mound, Howard River estuary, Darwin (Site G, Jan. 2002); **C**, burrow of *P. darwini* excavated in mud accumulated between rocks, Channel Island (Site I, July 2001); **D**, *P. darwini* perching on an exposed aerial root of *Rhizophora stylosa*, Channel Island (Site I, July 2001).

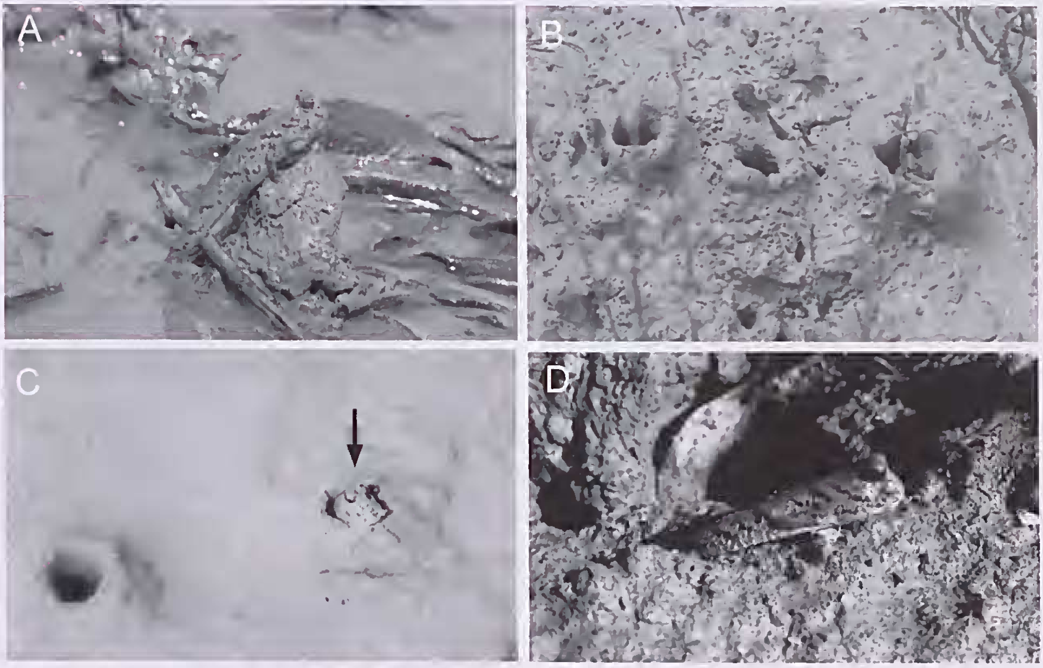

Fig. 7. *Periophthalmus minutus.* **A**, *P. minutus* on wet mudflat, Middle Arm, Port Darwin (Site J, Feb. 2004); **B**, turreted burrow openings on mudflat, Howard River estuary, Darwin (Site H, Mar. 2001), with individual (arrow) emerging; **C**, *P. minutus* (arrow) about to emerge from its burrow before the ebbing tide uncovers the burrow opening, Middle Arm, Port Darwin (Site J, July 2001); **D**, *P. minutus* sitting on relatively dry mud, Middle Arm, Port Darwin (Site J, Nov. 2000).

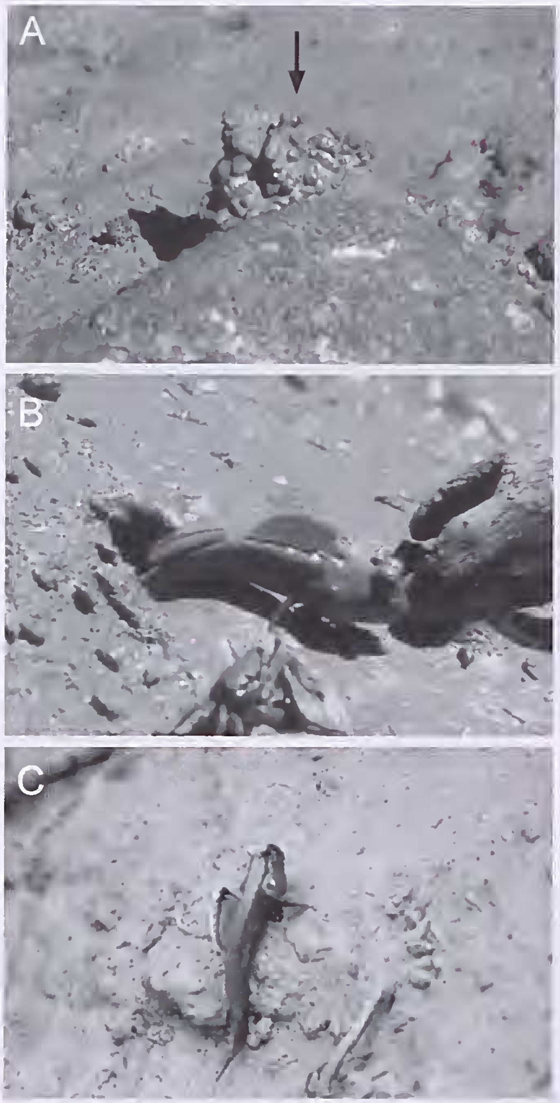

Fig. 8. *Periophthalmus novaeguineaensis*. **A**, *P. novaeguineaensis* (arrow) about to come out of its burrow by boulder, Derby Harbour (Site M, July 2002); **B**, *P. novaeguineaensis* displaying threat posture to a crab by its burrow opening in mangrove forest, near Derby (Site O, Feb. 2003); **C**, male *P. novaeguineaensis* performing a courtship display on the same mud mound (Site O, Feb. 2004).

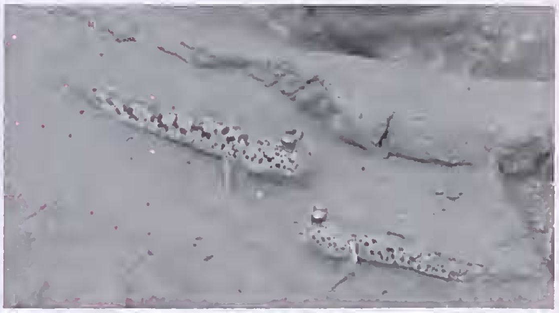

Fig. 9. *Periophthalmus takita* at Ludmilla Creek, Darwin (Site E, Feb. 2004).

landward border. Site H was also high but was subjected to an unpredictable emersion/submersion cycle due to discharge from nearby fish-ponds. Juvenile *B. birdsongi* were often observed together with *P. minutus* in shallow tidepools remaining after the ebb tide. Burrows of *P. minutus* had two or three turrets above the mud surface (Fig. 7B) as did those of *P. argentilineatus* (Fig. 5A). *Periophthalmus minutus* moved around the habitat during the low tide period; some travelled 5 m or more from their burrow, but most individuals stayed closer. *Periophthalmus minutus* confined themselves in burrows during habitat submersion, and came out of the burrows when the water receded to the depth of 1 to 2 cm (Table 4, Fig. 7C), although a few individuals remained perched on mangrove trunks during high tide. During neap tide in the dry season when the *P. minutus* habitat remained exposed and dry for more than 10 days, very few *P. minutus* were observed resting on the mudflat (Fig. 7D); most remained within their burrows until the next spring tide or rain inundated the habitat. The water salinity of *P. minutus* burrows measured as high as 75 ppt in November 2000, when daily maximum temperature was 30–35°C and the rainy season was about to start toward the end of the month (http://www.bom.gov.au/climate/data/index.shtml). Courtship behaviour was seen in February 2003 (by Dr. K. Soyano of Nagasaki University) and many juveniles of 30 mm TL or less were present on the mudflat in February 2003 and March 2001 (Table 4).

Periophthalmus novaeguineaensis. *Periophthalmus novaeguineaensis* also inhabited the highest intertidal location, but in areas of irregular topography (Table 2).

Table 4. Burrow confinement during high tide and months when reproductive behaviour and the occurrence of juvenile fish were observed for nine species of mudskippers collected in northern Australia. CA, Cairns; DA, Darwin; DE, Derby; *Courtship display, #Biparental burrow tending.

	Burrow confinement of adult fish during high tide	**Reproductive behaviour confirmed**	**Juvenile fish occurrence**
Boleophthalmus birdsongi	Yes	*Aug.and Nov. (DA)	Mar., Jul., and Nov. (DA)
Boleophthalmus caeruleomaculatus	Yes	*Jul. (DE)	Mar. (DA) and Jul. (DA, DE)
Periophthalmodon freycineti	Probably no	#Nov. (CA)	Mar. (CA)
Periophthalmus argentilineatus	Probably no	?	?
Periophthalmus darwini	Probably no	?	Feb. (DA)
Periophthalmus minutus	Yes	*Feb. (DA)	Feb. and Mar. (DA)
Periophthalmus novaeguineaensis	Yes	*Feb. (DE)	?
Periophthalmus takita	Probably yes	*Jul. (DA)	?
Scartelaos histophorus	Yes	*Mar. and Nov. (CA), Jul. (DE)	?

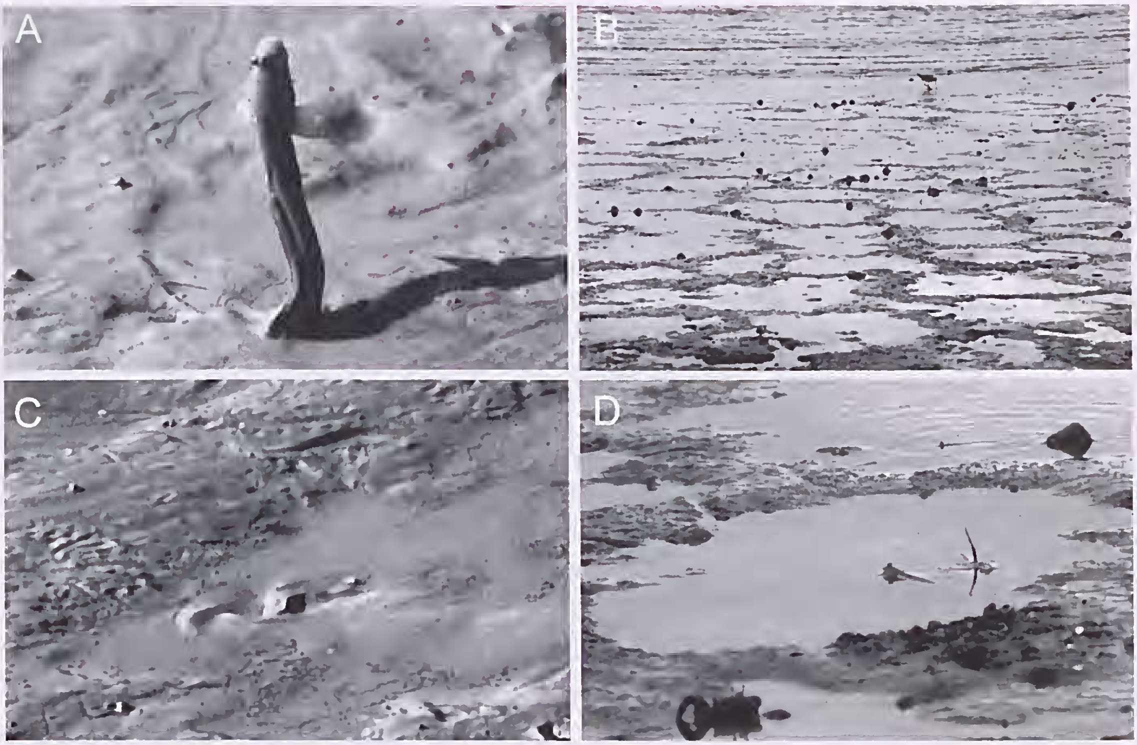

Fig. 10. *Scartelaos histophorus* at Esplanade Beach, Cairns (Site C, Nov. 2000). **A**, male performing a tail-stand; **B**, territories with peripheral mud rims; **C**, male twisting its body in the soft mud, constructing a mud rim; **D**, pair (male and female) of *S. histophorus* in their walled territory.

Periophthalmus novaeguineaensis changed its distribution during our survey of the Derby coast: the species inhabited a muddy beach at Site M in July, 2002, where boulders of various sizes were strewn in the mud (Fig. 1M), but was rare in February 2003 and 2004. Due to this rarity, we searched nearby areas and found that this species was abundant at Site O (Fig. 1O) in a mangrove forest, only about 200 m from Derby Harbour. Burrows of *P. novaeguineaensis* were found mainly under boulders but also in mud several metres away from them at Site M in July (Fig. 8A) and on steep mud mounds at Site O in February (Fig. 8B). Individuals foraged around their burrows and retreated into the burrow when frightened and while the burrows were flooded during high tide (Table 4). In February, some males exhibited a dark body colour (Fig. 8C) and performed courtship displays typical of species of *Periophthalmus* around their burrows (Polunin 1972; Matoba & Dotsu 1977; Brillet 1980; Baeck *et al.* 2008; Table 4).

Periophthalmus takita. *Periophthalmus takita* (Fig. 9) inhabited the lower intertidal zones (Table 2). The fish was the most dominant among the *Periophthalmus* species, and was observed on every low, wet and soft mudflat in Darwin. *Periophthalmus takita* was syntopic with *B. birdsongi* at Site E, and with *B. birdsongi*, *B. caeruleomaculatus* and *S. histophorus* at Site F. During habitat submersion, none or only a few *P. takita* were found emerged, suggesting their confinement in a burrow (Table 4). Courtship displays including jumping and body waving, typical among *Periophthalmus* species, were observed in July, 2001, on the mudflat in Site F (Table 4).

Scartelaos histophorus. This species inhabited soft, wet and level mudflats located low in the intertidal zone along the shore or on estuarine banks (Table 2). All individuals take refuge in burrows to shelter from predators and during high tide (Table 4). This species was often syntopic with *Periophthalmodon freycineti* at Site C and with *B. birdsongi*, *B. caeruleomaculatus* and *Periophthalmus takita* at Site F. It is possible to discriminate the sex of paired individuals on the basis of the male's larger body size and longer DF1 length (Fig. 10D; Townsend & Tibbetts 2005). Often, individuals of *S. histophorus*, smaller than territorial males and presumably consisting of females and young males, aggregated in pools, but it was not possible to determine their sex by field observation. Larger males were territorial, but paired females were not observed to defend territories. These large males kept territories of approx. 50–80 cm in diameter around the burrow. Male *S. histophorus* were observed to form a peripheral mud rim around their territories when density was high at Site C in November, 2000 (Fig. 10B). A territory owner repeatedly twisted his body on the mud, pushing the softened mud behind him by his tail (Fig. 10C), piling up the mud on the periphery of the territory. The mudflat area containing mud-rimmed territories extended more than 100 m along the shore. The frequency of rimmed territories decreased as the population density decreased, and they had completely disappeared by January 2002. Territorial males performed a unique courtship display ('tail-standing'; Fig. 10A), a jump that lifts most of the body up onto the tail; these displays were sighted in March, November (and December, HKL pers. obs.) in Cairns and in July in Derby (Table 4). Male *S. histophorus* frequently had violent confrontations with neighboring males, repeatedly performing the courtship display.

DISCUSSION

Species Occurrence. All nine mudskipper species identified in this study had previously been reported from northern Australia (Murdy 1989; Larson & Takita 2004; Hoese & Larson 2006; Jaafar & Larson 2008). The species reported as *Periophthalmodon schlosseri*, *Periophthalmus vulgaris* Eggert and *Periophthalmus expeditionium* Whitley by Milward (1974) and Nursall (1981) have been identified by us as *Periophthalmodon freycineti*, *Periophthalmus argentilineatus* (see Murdy 1989) and *P. novaeguineaensis*, respectively (but this is not absolutely certain as no specimens are available from these early studies). *Periophthalmus darwini* was described as a new species on the basis of specimens collected in the early part of this study (Larson & Takita 2004). *Periophthalmus murdyi* is a junior synonym of *P. novaeguineaensis* (Jaafar & Larson 2008).

On the other hand, the species which had been identified as *P. novaeguineaensis* by Murdy (1989) and Larson & Takita (2004), was found to be a new species and subsequently named as *P. takita* (Jaafar & Larson 2008). Four oxudercine species previously reported from northern Australia were not found during this study, i.e. *Apocryptodon madurensis* (Bleeker), *Oxuderces wirzi* (Koumans), *Periophthalmus kalolo* Lesson and *Periophthalmus weberi* Eggert (Milward 1974; Nursall 1981; Murdy 1989; Larson & Williams 1997; Larson 2008). The first two species inhabit very specific soft mud habitats (they 'swim' through soft mud with only the eyes exposed); the *P. kalolo* record is a misidentification (due to inadequate literature) and *P. weberi* inhabits strongly freshwater-influenced habitats (Larson 2008; Larson & Williams in prep.). Polgar *et al.* (2010) found nine species of oxudercine gobies from the region of the lower Fly River and delta, Papua New Guinea. Of these, seven were also collected by us and two others were previously confirmed as occurring in Australia (Murdy 1989), suggesting a similarity in mudskipper fauna between Australia and southern Papua New Guinea.

The most useful feature for identifying congeneric mudskipper species is the colour pattern of the fins and body (Murdy 1989). However, information on mudskipper colour pattern is usually not provided in sufficient detail in taxonomic papers, as they usually deal with fixed specimens that have lost their live colouration soon after fixation. For this reason, knowledge of live adult mudskippers presented in this paper is crucial for field biologists investigating mudskipper ecology and behaviour in their natural habitat, where collecting study material for species identification is often very difficult. An important source of information that we are unable to provide is the colour pattern of juveniles for most species. In fact, juveniles of *Periophthalmus* species were quite difficult to identify, unless the distribution of the species was geographically isolated, as diagnostic colour patterns are not exhibited by juveniles. A few publications describe the morphology of mudskippers during early development and/or juvenile stages (e.g. Kobayashi *et al.* 1972), but they rarely refer to live body colour. Drawings of fixed specimens are of limited use for field identification of juveniles. Baeck *et al.* (2008) illustrated species-specific differences in the fin colour between juveniles of two Korean *Periophthalmus* species (*P. magnuspinnatus* Lee, Choi & Ryu and *P. modestus* Cantor), which can be distinguished only when the fish are 40 mm or greater in body length.

Our data on the mudskipper distribution in northern Australia may have been biased, for the following reasons. Firstly, there were differences in the frequency and duration of our field surveys between localities; the surveys were mainly conducted in well-developed mangrove forests and mudflats in or near Darwin, but less frequently in Cairns and Western Australia (Table 1) due to greater difficulties in sampling. Secondly, investigations in soft mudflat habitat, which is often located between or besides thick mangrove forests, are usually difficult to conduct, as discussed in a study on mud-dwelling amblyopine fish (Murdy & Shibukawa 2000). On the relatively isolated coasts of northern Australia, access is often not easily gained for mudskipper (or any other) surveys. Lastly, the behaviour of mudskippers of rapidly retreating in response to any disturbance renders fish collection a difficult task.

These factors possibly explain our failure in sampling some species previously known from Northern Territory (see above). In addition, mudflats are extremely dynamic habitats, being continually influenced by weather conditions and human activities (Nursall 1981; Takita *et al.* 1999). The transient and sometimes ephemeral nature of mudflats may also be responsible for some inconsistent records of mudskipper distribution in the literature, while settlement and recruitment dynamics may cause frequent population changes as previously observed for some mudskippers (Milward 1974; Townsend & Tibbetts 1995). The habitat shift observed for *Periophthalmus novaeguineaensis* seems not to be attributed to any apparent environmental alterations. Investigations into detailed analyses of physicochemical conditions, recruitment changes and distribution of prey and predator organisms in mudskipper habitats may give a clue to the answer to these questions.

Habitat Condition. Habitat conditions of the mudskippers studied are summarised in Table 2. Similar accounts on habitat topography and zonation in intertidal zones have also been provided for Australian (Nursall 1981) and Malaysian mudskippers (e.g. Polgar & Crosa 2009). Habitat separation of mudskippers in the intertidal zone may be explained by different physiological capacity to withstand prolonged emersion, different tactics of predator avoidance (Polgar & Crosa 2009), the need for water after prey capture (Stebbins & Kalk 1961; Gordon *et al.* 1978), preference for substrate characteristics, different feeding preference (i.e., herbivory, omnivory versus carnivory), or different environmental requirements with development. The general pattern of mudskipper vertical distribution in tidal flats has been assumed to be: "Species of *Apocryptes* and *Scartelaos* are considered to live in very soft mud around mean sea level while *Boleophthalmus* spp. are found higher on the shore. The distributions of *Periophthalmus* and *Periophthalmodon* spp. are at the level of the highest tides and beyond" (Clayton 1993). However, some of our observations are in conflict with this generalised pattern: juvenile *B. birdsongi* co-occupied the highest intertidal zones together with *P. minutus*, while *P. takita* inhabited the lower zones where *Boleophthalmus* usually dominate.

Through analysis of seven mudskippers in Malaysia, Polgar & Crosa (2009) found that the habitats of *Periophthalmus chrysospilos* Bleeker were more similar to the habitats of *Boleophthalmus* species (*Boleophthalmus boddarti* and *B. pectinirostris* (Linnaeus)) and *S. histophorus*, than to the habitats of other *Periophthalmus* and *Periophthalmodon* species that they studied (*Periophthalmus gracilis* Eggert, *P. variabilis* Eggert and *Periophthalmodon schlosseri*). It seems likely that no single factor can explain spatial distributions of different mudskippers, but rather a combination of local biotic and abiotic factors would have significant influence on how different species segregate their habitats in an environmental gradient of mudflats (e.g. Clayton 1993).

Of the nine mudskipper species collected in this study, *Periophthalmus darwini*, *P. minutus* and *P. novaeguineaensis* occupied the highest intertidal zone and therefore are presumed to have the highest capacity for life under semi-terrestrial conditions. Unfortunately, comparative physiological data are unavailable for these three *Periophthalmus* species, but they are presumably capable of maintaining respiratory, acid-base and osmoregulatory homeostasis with limited access to water. Preliminary evidence we obtained for mudskippers' tolerance to high salinity is that the water salinity in *Periophthalmus minutus* burrows was as high as 75 ppt during a hot dry season. Thus, this species, and possibly also *P. darwini* and *P. novaeguineaensis*, is thought to have the osmoregulatory capacity to withstand these extreme hypersaline conditions. Unpublished data by Takeda *et al.* in fact demonstrated that *P. minutus* can maintain plasma sodium concentration during a 9 to 14 day exposure to 200% seawater. Burrows were only partially filled with water during neap tide in the dry season and most individuals remained above the water table in globular chambers 3 to 6 cm deep from the burrow openings during that period (Takeda *et al.* unpublished). This observation indicates that individuals of *P. minutus* avoid exposure to high salinities inside their burrows. However, such tactics may further stress the physiological status of the fish when emersion is prolonged.

Habitat preference differs even among the three species living in the highest intertidal zone. *Periophthalmus darwini* and *P. novaeguineaensis* inhabited mudflats with rough topography whereas *P. minutus* always occurred on flat, exposed and relatively smooth mudflats. This difference may be due to behavioural, rather than physiological, differences in species-specific tactics they employed to avoid predators. *Periophthalmus darwini* and *P. novaeguineaensis* occupied areas where suitable shelters were abundant and the fishes took refuge under stones or moved quickly into the mangrove vegetation when an observer came near. In contrast, *P. minutus* inhabited open mudflats, where avian predation risk may be higher. The species' high affinity for burrows may be an adaptation for survival in open mudflats. Where habitats were covered by halophytes or located near a mangrove forest, *P. minutus* often remained under cover of the vegetation or moved well into the forest when alarmed.

Where *P. novaeguineaensis* and *P. darwini* were syntopic, they occupied different microhabitats. At Site O in Derby, *P. novaeguineaensis* occurred evenly over the surface of a mud mound, while *P. darwini* was restricted to the higher part of the mound. This may be explained by the need for water access immediately after feeding, as described for some *Periophthalmus* species (Stebbins & Kalk 1961; Gordon *et al.* 1978; Sponder & Lauder 1981). *Periophthalmus novaeguineaensis* was seen to visit pools on the flat wet surface after each capture of a prey item on the mud mound, whereas *P. darwini*, foraging high on the mud mound, was not seen to make a descent to water after feeding. The highest area of the mud mound and the mangrove forest floor inhabited by *P. darwini* was relatively dry, apparently with very limited water availability. Similarly, water availability seemed limited during low tide in the *P. darwini* habitat on the rocky shore at Channel Island. Where *P. darwini* was the only *Periophthalmus* species present (Howard River estuary), they occupied the entire surface of a mud mound, suggesting that larger *Periophthalmus* species may limit the distribution of the smaller *P. darwini*.

Reproduction of *Periophthalmus darwini*, *P. minutus* and *P. novaeguineaensis* is inferred to occur during the rainy season, as the occurrence of juveniles was confirmed for the former two species and courtship displays were sighted for the last species only during the middle of the rainy season, although *P. novaeguineaensis* habitat was visited only in February and July. These mudskippers spend their whole life at the highest location where environmental conditions are presumably more formidable for embryo incubation and early development.

The habitat separation observed for juvenile and adult *B. birdsongi* (Table 2) is puzzling. Polgar *et al.* (2010) also reported that juvenile *Boleophthalmus* sp. (possibly a new species) were found in more terrestrial conditions than adults. It is unlikely that juveniles have a higher capacity for sub-aerial existence than adults. Habitat separation with development was proposed for both *Periophthalmodon freycineti* and *P. schlosseri* by Murdy (1989). Nursall (1981) observed smaller sized *P. freycineti* (as *P. schlosseri*) avoiding larger individuals.

Lifestyles and Burrowing. Table 4 summarises occurrence of burrow confinement of adult fish during high tide, reproductive behaviour (courtship display or biparental care) and the months that we confirmed the occurrence of juvenile individuals for the nine mudskipper species. All *Boleophthalmus* species appear to maintain a burrow (*Boleophthalmus boddarti* (Pallas) (Murdy 1986); *B. pectinirostris* (Dotsu & Matoba 1977); *Boleophthalmus dussumieri* Valenciennes (Clayton & Vaughan 1988; as *B. boddarti*)). *Boleophthalmus birdsongi* and *B. caeruleomaculatus* emerged from their burrows when the tide receded, and performed territorial behaviour on mudflats, similar to that known for *B. dussumieri* (Clayton & Vaughan 1982; as *B. boddarti*) and *B. pectinirostris* (Dotsu & Matoba 1977; Chen *et al.* 2007). Male *S. histophorus* also dig and maintain burrows and are territorial. Neither burrow excavation nor territorial behaviour were observed for female *S. histophorus*.

Periophthalmus species are more diverse with respect to burrow behaviour and confinement therein during high tide (Table 4). Those species that make burrows and confine themselves during high tide include *P. minutus* and *P. novaeguineaensis*. *Periophthalmus takita* also takes refuge in burrows, which may or may not be 'owned' by the fish. It is unlikely that *P. darwini* uses its burrows as refuges during high tide. Burrow confinement was not confirmed for *P. argentilineatus*, which was often seen in an exposed position on the substrate or perched on a rock. *Periophthalmus argentilineatus* was seen to migrate across the tidal flat during incoming tides in Cairns, Darwin and Broome, as was observed for the same species on east African mudflats (Gordon *et al.* 1968; Colombini *et al.* 1995: as *Periophthalmus sobrinus* Eggert) and for other *Periophthalmus* species, *Periophthalmus modestus* (Matoba & Dotsu 1977: as *Periophthalmus cantonensis* (Osbeck)) and *P. chrysospilos* (see Polgar & Crosa 2009).

At Okinawa, Japan, tidal migration of *P. argentilineatus* was presumed on the basis of burrow locations on the mangrove floor 27.9 ± 1.2 cm high above standard sea level (Oshiro *et al.* 2005). The lack of burrow confinement in *P. argentilineatus* (as *P. sobrinus*) observed by Colombini *et al.* (1995) on the mangrove banks of the Tana River delta in Kenya, where it was recorded that "... the mudskippers always abandoned the occasional burrows on the incoming spring tide...and never remain submerged during high tide" has not been verified in this study. On the basis of the mean hourly zonation at spring and neap tide, these authors stated "The data show that at spring tide the mudskippers escape from the water but tend to remain under cover of the vegetation". Polgar & Crosa (2009) observed that *Periophthalmus chrysospilos*, *P. gracilis* and *P. variabilis* from Malaysia formed a group that avoids water when reached by the incoming tide, together with *Periophthalmodon schlosseri*. *Periophthalmus modestus*, a temperate mudskipper, appears to spend the high tide period on the ground when the air temperature is high (Ikebe & Oishi 1996, 1997; Baeck *et al.* 2008).

Tropical or subtropical mudskippers that take refuge in burrows during high tide under high temperature conditions may store air as an oxygen reservoir to survive severely hypoxic burrow conditions, as inferred from air storage for embryonic development demonstrated for *Periophthalmodon schlosseri* (Ishimatsu *et al.* 1998, 2009) and *Periophthalmus modestus* (Ishimatsu *et al.* 2007). Burrow confinement was not confirmed for *Periophthalmodon freycineti* (Table 4). The lifestyle of *P. freycineti* observed in this study is similar to that of *P. schlosseri* with respect to burrowing, foraging, swimming and conspecific confrontation (Hora 1936; MacNae 1968; Murdy 1986). MacNae (1968) speculated that *P. schlosseri* confined itself in its own burrow during high tide. *Periophthalmodon freycineti* was often found during high tide hiding itself under grasses along the water's edge on the shore or stream bank.

Territory of *Scartelaos histophorus*. Territories with mud rims have been known in *S. histophorus* (as *Scartelaos viridis* (Hamilton)) in southern China, although their structure or construction behaviour has not been described (Yang *et al.* 2003). The mud rims in the territories of *S. histophorus* were constructed by males when fish density was extremely high. Since frequent confrontations took place between neighbours while territory owners repeatedly performed typical courtship jumps, there is no doubt that *S. histophorus* constructs the mud rims as 'fences' to protect the mating space from invasion by neighbouring males. Townsend & Tibbetts (2005) reported territoriality of *S. histophorus* in shallow water pools with descriptions of agonistic and tail-stand behaviour. These authors also reported body motion displacing the substratum as we observed, but did not mention mud rims, probably because of low fish population. The construction of territories with mud rims is known also in *B. dussumieri*, but with different building behaviour (Clayton & Vaughan 1982; as *B. boddarti*). *Boleophthalmus dussumieri* discharges mouthfuls of mud onto the territorial periphery, presumably to secure food and to reduce agonistic confrontations with conspecific neighbors when fish density is high (Clayton 1987). Territories with peripheral mud walls are also known in *B. pectinirostris* cultured in ponds (Chen *et al.* 2007), although construction behaviour was not described.

ACKNOWLEDGEMENTS

The field surveys were supported by the Museum and Art Gallery of the Northern Territory, Australia. Our thanks are due to Mr Bill Boustead of Darwin, who allowed us to carry out surveys in his fish ponds and use his facilities.

Mr Gavin Dally, Mr Steven Gregg and Mr Rex Williams of the Museum and Art Gallery of the Northern Territory, Dr Tatsusuke Takeda of the Faculty of Agriculture, Kyushu University, Dr Kiyoshi Soyano of Institute for East China Sea Research, Nagasaki University, and students of the Faculty of Fisheries, Nagasaki University, helped us in the field surveys. Mr Jeff W. Johnson of the Queensland Museum helped us in examining mudskipper specimens at the Museum. Dr Ed Murdy and Dr Gianluca Polgar reviewed the manuscript and made many helpful comments. This study was financially supported by the Ministry of Education, Culture, Sports, Science and Technology, Japan (Grant-in-Aid no. 15405028).

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Accepted 29 September 2011

S-1152